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Short Communication

The structure of the pawpad lamellae of four *Rattus* species

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The structure and function of the pawpad lamellae of *Rattus* species relate directly to their behavior (Brooks and Rowe 1987). Thus the pawpads of climbing species such as the roof rat, *R. rattus*, have evolved numerous lamellae to provide better gripping and clinging power, whereas digging species such as the Norway rat, *R. norvegicus*, have smooth pawpads. Pawpads have only been described previously, however, as either finely lamellated or nearly smooth (Musser 1973, Marshall 1977, Corbet and Hill 1992), and no detailed studies of the structure of the lamellae have been carried out. In this paper, we describe the histological features of the lamellae and relate them to the differing behaviors of two climbing *Rattus* species (*R. rattus* and the Polynesian rat, *R. exulans*) and two digging species (the ricefield rat, *R. argentiventer* and *R. norvegicus*).

Materials and Methods

Specimens of *R. rattus* and *R. norvegicus* from Japan, and of *R. exulans* and *R. argentiventer* from Indonesia and Thailand were used in this study. The majority of these specimens were laboratory reared in Miyazaki Medical College and Ikari Corporation with the remainder killed just after capture in fields or buildings.

The largest pawpads were those of the outer metatarsals so these were removed for lamellar analysis. Pawpads were surgically excised, fixed in 10% formalin, washed in tap water and dehydrated in a graded series of ethanol. Specimens were then immersed in isoamyl acetate and dried with liquid CO_2 in a critical point dryer. They were mounted on a scanning peg using a piece of conductive tape coated to 30 nm with gold-palladium in a DC sputtering apparatus, and observed at 10 kV in a JSM 5400LV scanning electron microscope (SEM). Microscopic photographs were taken at a magnification of 100.

Histological preparations were made from pads fixed in 10% formalin. The fixed pads were removed from the hind feet and embedded in paraffin using standard histological procedures. The pads were cut into serial sections

vertical to the lamellae at 8-10 μm intervals and stained with hematoxylin-eosin. One serial section from the middle part of the pad was selected for detailed examination and measurements. The height and width of the lamellae were measured with an ocular micrometer. The image was then projected onto a screen and the angle of the lamellae was measured with a protractor. The maximum height of the stratum corneum was defined as Ch, the maximum width of lamellae as Lw, and the average angle of 10 pits on corneous, lucid or granular layers as θ in radians (Fig. 1). Because the pits on the corneous layer were often split, those on the lucid or granular layers were more suitable for measuring angles from. The lamellae on the front of the pawpads were excluded from these measurements because they often had irregular pit angles, width and height. Values of Ch, Lw and θ from 10 specimens were averaged for each species. Statistical analyses of these values were made by using the Kruskal-Wallis analysis of variance of ranks followed by the Tukey test.

Results and Discussion

Among mammals, the pattern of the peculiar outer surface of the corneous layer is generally affected by the lower epidermal layers and the dermis (Sokolov 1982). The four species of *Rattus* also have lamellae consisting of a superior corneous layer (stratum corneum) parallel to the underlying lucid (stratum lucidum) and the granular (stratum granulosum) layers (Fig. 1). Pit angles from the lucid or granular layers could therefore be substituted for those from the corneous layer. Keratin plates of the corneous layer were found to be arranged in columns as was suggested by Sokolov (1982), and each lamella was distinguishable in the columns.

Both histological sections and SEM photographs showed that whereas *R. rattus* and *R. exulans* had extemely-developed lamellae, *R. argentiventer* had moderately-developed lamellae and *R. norvegicus* had only poorly-developed lamellae (Figs. 1 and 2, Table 1). The Kruskal-Wallis analysis of the four species revealed significant differences among them in Ch ($d.f.=3$, corrected $H=11.0$, corrected $p<0.05$), Lw ($d.f.=3$, corrected $H=18.5$, corrected $p<0.01$), and θ ($d.f.=3$, corrected $H=31.6$, corrected $p<0.01$). The Tukey tests showed that *R. rattus* had significantly greater Ch's than the three other species (Studentized range $Q=3.80$, $d.f.=36$, number of treatments $a=4$, $p=0.05$, significant difference $D=81.4$), while *R. norvegicus* had significantly greater Lw's than those of the other species ($Q=3.80$, $d.f.=36$, $a=4$, $p=0.05$, $D=30.5$). The mean pit angles (θ) were in the order: *R. rattus* = *R. exulans* > *R. argentiventer* > *R. norvegicus* ($Q=3.80$, $d.f.=36$, $a=4$, $p=0.05$, $D=0.32$), which confirmed the observations made with the SEM.

Musser (1973) had noted that the pawpads of digging *Rattus* species were flush, whereas those of good climbers such as *R. rattus* protruded from the sole. This study has confirmed that the prominent pawpads of *R. rattus* are due to the thick corneous layer. It appears therefore that among *Rattus* spp. good climbers have prominent pawpads or a thick corneous layer as well as finely

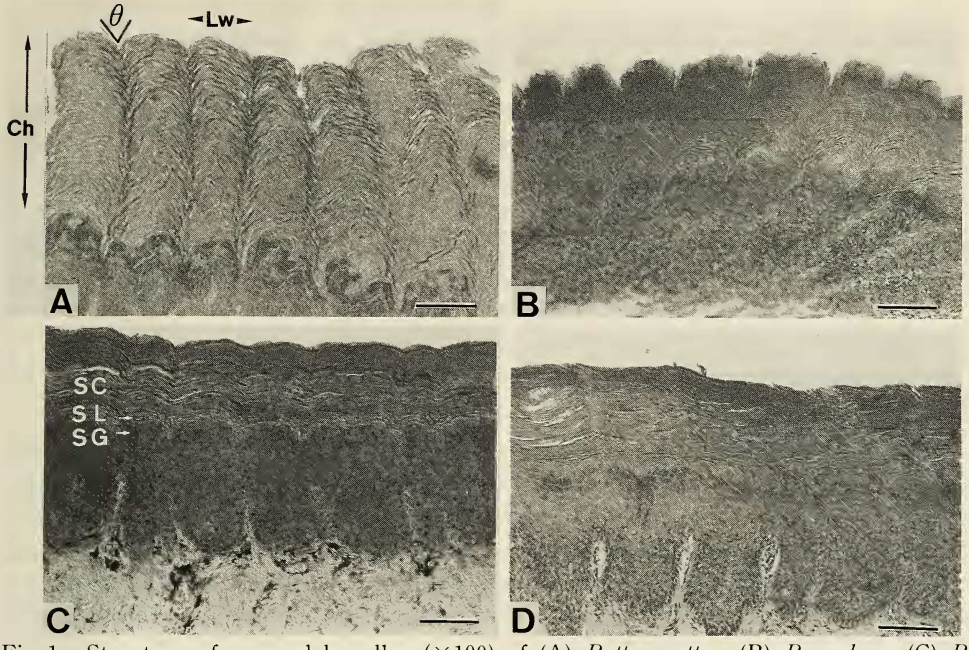

Fig. 1. Structure of pawpad lamellae (×100) of (A) *Rattus rattus*, (B) *R. exulans*, (C) *R. argentiventer* and (D) *R. norvegicus*, showing measurements taken. The scale indicates 100 μm. SC: stratum corneum, SG: stratum granulosum, SL: stratum lucidum, Ch: height of corneous layer, Lw: width of lamella, θ: angle of pit on lucid or granular layers.

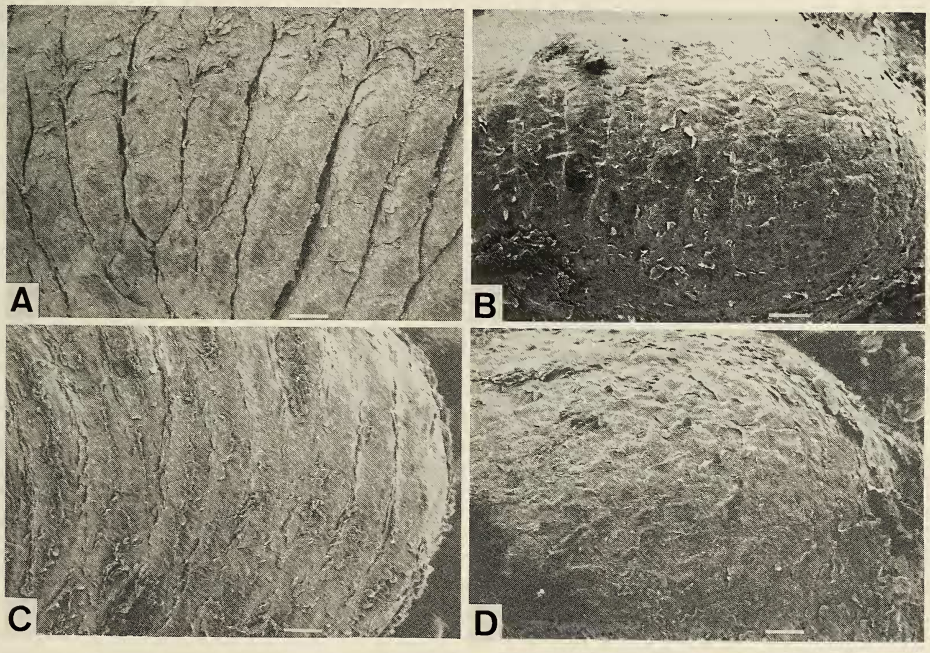

Fig. 2. SEM photographs (×100) of pawpad lamellae of (A) *Rattus rattus*, (B) *R. exulans*, (C) *R. argentiventer* and (D) *R. norvegicus*. The scale indicates 100 μm.

Table 1. Maximum height of corneous layer (Ch), maximum width of lamellae (Lw), and average pit angle between lamellae (θ) of the pawpads of four *Rattus* species.

Species	n	Ch±SD (μm)	Lw±SD (μm)	θ±SE (radian)
R. rattus	10	303±73[a]	137±21	1.06±0.17
R. exulans	10	200±67	123±21	1.08±0.16
R. argentiventer	10	203±45	153±20	1.93±0.35[a]
R. norvegicus	10	216±69	185±32[a]	2.66±0.07[b]

[a] Significantly larger than the others except "b" in the same column ; [b] significantly larger than "a" (Tukey test, $p=0.05$).

lamellated pawpads. These finely lamellated pawpads have steep lamellar pits and narrow lamellae : the steeper the lamellar pits and the narrower the lamellae, the more grip they provide for clinging or climbing.

In conclusion, our examination of the histological features of *Rattus* pawpad lamellae has shown that they differ in structure corresponding with the behavior of the species. The pawpads of digging species such as *R. norvegicus* are characterized by a thin corneous layer, shallow lamellar pits and broad lamellae. In contrast, the pawpads of climbing species such as *R. rattus* are characterized by a thick corneous layer, steep lamellar pits and narrow lamellae.

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